

THE RELATIVE IMPORTANCE OF HOST BEHAVIOUR, METHOD OF TRANSMISSION AND LONGEVITY ON THE ESTABLISHMENT OF AN ACANTHOCEPHALAN POPULATION IN TWO REPTILIAN HOSTS.

CHRISTOPHER B. DANIELS

Daniels, C.B. 1990 09 20: The relative importance of host behaviour, method of transmission and longevity on the establishment of an acanthocephalan population in two reptilian hosts. *Memoirs of the Queensland Museum* 29(2): 367-374. Brisbane. ISSN 0079-8835.

The acanthocephalan parasite *Sphaerechinorhynchus rotundocapitatus* occupies the rectum and large intestine of the riparian Australian snake, *Pseudechis porphyriacus*. Eggs are released into water to be consumed by an aquatic arthropod (intermediate host) which in turn is captured by the eastern water skink, *Eulamprus quoyii* (transport host). The parasite adopts a resting, encysted stage in both hosts until the lizard falls prey to the snake. *Pseudechis porphyriacus* exhibits a relatively high frequency of infection but *E. quoyii* comprises only 2% of prey items. Aquatic prey also represent only a small proportion of the diet of *E. quoyii*. Unlike all other acanthocephalans so far examined, there is no evidence that the parasite alters intermediate host behaviour or physiology to increase the chance of capture by the next host in the life cycle. Rather, the operation of the food web appears to provide sufficient momentum to transfer the parasite from one stage to the next, provided both the hosts and the parasite are long lived. Transfer mechanisms involving parasite mediated alterations in host behaviour can be termed 'active' while those which do not significantly affect a host are termed 'passive'. The advantages of passive transfer mechanisms are discussed. □ *Parasite, lizard, snake, invertebrate, Acanthocephala, life cycle, passive transport, mathematical model.*

Christopher B. Daniels, Department of Physiology, School of Medicine, Flinders University of South Australia, Bedford Park, South Australia 5042, Australia; 12 July, 1988.

Almost all parasites with multistage lifecycles often rely for transmission on the predation of their intermediate host by their final host. However, usually only a small proportion of intermediate hosts (infected or otherwise) are captured by predators. Thus, sometimes natural selection influences parasites to alter intermediate host behaviour to increase the chance of capture by the final host. Many such parasites produce extreme and often spectacular alterations in intermediate host behaviour to move the prey into the feeding niche of the final host and/or decrease the frequency of predation by other inappropriate carnivores (e.g. Holmes, 1976; Moore, 1984). Holmes (1976) suggested that if the final host is an efficient predator, the strategy of the parasite should be to make the prey more conspicuous, and when the predator is inefficient the parasite should make the prey more conspicuous and easier to catch. In both cases the parasite may either institute novel behaviour patterns or simply elicit pre-existing host behaviours under inappropriate conditions (Moore, 1984).

In cases where the parasite interacts with, and

influences, host behaviour to promote transmission, the methods employed can be termed 'active'. Mechanisms whereby parasites promote their own transmission without influencing host behaviour or physiology can be termed 'passive'. Thus, increasing parasite longevity and reproductive output may 'passively' promote transmission by increasing the number of infective individuals which can contact hosts. Digeneans amplify their numbers in intermediate hosts by producing cercariae highly adapted for transmission. Active interactions between parasites and their hosts have received considerable attention recently from behavioural, physiological, evolutionary and genetic viewpoints (Holmes and Bethel, 1972; Bethel and Holmes, 1973, 1974, 1977; Clarke, 1979; Smith-Trail, 1980; Brassard et al. 1982; Rand et al. 1983, Schall, 1983) as well as in studies of population dynamics (Holmes, 1982). However, this study will show: (1) the importance of passive forces in influencing a parasite life cycle; (2) present a simple model to illustrate how selection can act on passive mechanisms to increase the probability of parasite transmission

from one host to the next; (3) present an example where an apparently active interaction between a parasite and its host in fact represents a method of passive transmission; (4) discuss the advantages and disadvantages of active and passive transmission techniques.

The system examined involves an acanthocephalan parasite of a snake. The parasite has two sequential intermediate hosts: an aquatic invertebrate and a riparian lizard. Because I have been unable to identify the invertebrate host and in order to test the 'worst case scenario', I will ignore any possible differences between the first and second intermediate hosts in the acanthocephalan life cycle. Behavioural changes in the first intermediate host are well documented but are relatively uncommon in the second host, possibly because parasites are usually associated with the first host for a longer period. However, in this system it will be demonstrated that while behavioural transformations in a host may improve the probability of transmission, such changes are not necessary for the successful establishment of the parasitic life cycle.

MATERIALS AND METHODS

This study applies aspects of the ecology of the acanthocephalan parasite *Sphaerechinorhynchus rotundocapitatus*, the eastern water skink *Eulamprus quoyii* and the red-bellied black snake *Pseudechis porphyriacus* to a simple probability model to test whether the parasite is utilising active or passive transfer mechanisms. More complex ecological and physiological studies of these animals are documented elsewhere (Shine 1975; Daniels, 1984; Daniels and Simbotwe, 1984) and only the salient characteristics will be present here.

Sphaerechinorhynchus rotundocapitatus

Sphaerechinorhynchus belongs to the order Palaeacanthocephala and contains two species both of which probably utilise snakes as final hosts (Schmidt and Kunz, 1966; Morris and Crompton, 1982). Palaeacanthocephala occupy the intestine of aquatic or semiaquatic vertebrates and their intermediate hosts are usually aquatic crustaceans, especially ostracods, amphipods or isopods (Crompton, 1970, 1975; Morris and Crompton, 1982). Palaeacanthocephalans sometimes utilise a second intermediate host, often a vertebrate (Morris and

Crompton, 1982). The second intermediate host of *S. rotundocapitatus* is the Australian skink *Eulamprus quoyii* which consumes infected intermediate hosts (currently unknown) and the lizards in turn are eaten by the final host (Daniels and Simbotwe, 1984).

The fully embryonated eggs of *S. rotundocapitatus* measure 0.07-0.09 x 0.025mm. These are released into water in the faeces of the snake, and are immediately infective and retain their infectivity for many months (Johnston and Deland, 1929a,b; Crompton, 1970, 1975). In most acanthocephalan life cycles the eggs are consumed by the correct arthropod host, hatch in the gut and the larval stage (acanthor) burrows through the intestinal wall to reach the haemocoel. The acanthor then develops into an acanthella and encysts. The encapsulated acanthella is termed a cystacanth (Crompton, 1970, 1975). Most of the cystacanths so far examined alter intermediate host behaviour which increase the likelihood of consumption by the final host (Holmes, 1976; Moore, 1984).

Infected arthropods are consumed by *E. quoyii*. The cystacanths hatch and the acanthellae again burrow into the peritoneum and encyst. Thirty four percent of 53 *E. quoyii* contained worms ($X = 2.0$, S.D. = 2.2, range 1-8), which measured up to 26mm long (Daniels and Simbotwe, 1984). Cystacanths were removed from the peritoneal wall, liver, outer gut wall, and sperm ducts. These can survive in the lizard for at least 6 months (Daniels and Simbotwe, 1984). Only 8% of juvenile *E. quoyii* were infected compared to 41.5% of adults (Daniels and Simbotwe, 1984). A few cystacanths have been recovered from other species of small lizard but not, to date, from frogs (Johnston, 1911, 1913; Johnston and Deland, 1929a; Daniels and Simbotwe, 1984).

Infected *E. quoyii* exhibited a mean voluntary diving time of nearly 8 minutes, while uninfected ones dived for an average of 4.5 minutes (Daniels, 1985a). Altering the voluntary diving time of *E. quoyii* may represent an active strategy promoting parasite transport because the red bellied black snake forages underwater and thus contacts more infected *E. quoyii* (Gilbert, 1935; Fleay, 1937; Shine, 1975). Twenty three percent of 22 *P. porphyriacus* contained adult *S. rotundocapitatus* in their rectum and lower large intestine ($X = 2.3$; S.D. = 2.3; range 1-7). Female worms measured up to 37mm while males exhibited a maximum length of 23mm (Johnston and Deland, 1929b).

Eulamprus quoyii

The eastern water skink, *Eulamprus quoyii*, is a common inhabitant of creek banks in eastern Australia (Veron and Heatwole, 1970; Spellerberg, 1972; Daniels, 1984). This lizard is territorial and intraspecifically aggressive (Done and Heatwole, 1977) often existing in dense populations. In the New England region of northern New South Wales, *E. quoyii* is active from September to May, and hibernates during the winter (Veron 1968, 1969b). Water skinks are viviparous, mate in October and the young are born in January/February (Veron, 1969b). Hatchlings are 35mm SVL (snout to vent length) and occupy fossorial habitats until they reach 55-80mm SVL. The juveniles then emerge and occupy suboptimal habitats, which are more exposed regions often some distance from water. Adults measure 80-110mm SVL and prefer rocky regions near expanses of water. Water skinks become sexually mature in their third year and live for 6-10 years (Veron, 1968, 1969b; Daniels, 1984).

Water skinks consume at least 25 taxa of prey including insects, worms, frogs, crustaceans, mammals, spiders, myriapods, snails, lizards and fish (Veron 1968, 1969a; Daniels, 1987). Approximately 25% of prey taxa are aquatic (Daniels, 1987). Of the aquatic prey items, the possible intermediate hosts of *S. rotundocapitatus* could be: Coleoptera (7.1% of the prey of *E. quoyii*), Hemiptera (2.9%), Odonata (3.8%), Plecoptera (2.2%), Crustacea (2.2%), Gastropoda (0.7%) or perhaps Anura (0.9% of prey taken by water skinks). Thus, whatever the immediate host, it must comprise less than 7% of the prey items of the transport hosts. A more realistic estimate is probably 1-2%. The most important prey items for *E. quoyii* are terrestrial Coleoptera (15% of prey) and ants which vary from 2% to 95% of the prey consumed depending on the season (Veron, 1969a; Daniels, 1987).

Water skinks can avoid predators by practising tail autotomy, with 49% of 110 New England lizards possessing regenerated tails (Daniels, 1985b). These lizards also exhibit a diverse range of escape tactics. Of 698 lizards chased by me around streams in New England, 32% escaped by swimming across open water to cover (rocks or reeds), 5% dived to the bottom of ponds and remained submerged and motionless for at least 2 minutes, while 61% ran to cover and 2% remained motionless (Daniels, 1984; Daniels and Heatwole, 1990).

Pseudechis porphyriacus

The red-bellied black snake *Pseudechis porphyriacus* is a large riparian elapid common in stream habitats in eastern Australia. In New England the snake is active from September to May with 5-8 young born alive in January/February (Shine, 1975, 1978). Hatchlings measure 24cm SVL and reach sexual maturity in their third year (Shine, 1978). Large snakes are 150cm SVL and at least 10 years old (Shine, 1975, 1978; Daniels, 1984). Red-bellied black snakes consume 34 types of prey including lizards, frogs, mammals, snakes and fish. Invertebrates are almost non-existent dietary items (Shine, 1977). Frogs comprise 82.4% of prey with *Limnodynastes tasmaniensis* the most common (16.9%). Water skinks are only 2% of the prey of *P. porphyriacus* (Shine, 1977). *P. porphyriacus* is an active forager and can capture prey on land or in water. The snakes will swim underwater for considerable periods in search of tadpoles, fish and other animals hiding amongst litter on the pond bottom (Gilbert, 1935; Fleay, 1937).

RESULTS AND DISCUSSION

If intermediate hosts comprise less than 7% of the diet of *E. quoyii* but 34% of *E. quoyii* are infected with cysts of *S. rotundocapitatus* and if *E. quoyii* comprise 2% of the diet of *P. porphyriacus* but 23% of *P. porphyriacus* are infected, then how can infection occur? One alternative is for the parasite to employ an active transfer mechanism. Some aspects of the behaviour of the transport host indicate this possibility. Parasitised lizards possessed much longer voluntary diving times than unparasitised ones and may be more likely to be captured by *P. porphyriacus* foraging underwater (Daniels and Simbotwe, 1984). However, it is unlikely that the parasite is exerting an active effect on the behaviour or physiology of *E. quoyii*, for a number of reasons. Firstly, an enhanced voluntary diving time may not necessarily indicate an increased tendency to use diving as the predominant escape method. Moreover, lizards rarely dived, with only 5% of individuals diving to avoid me (Daniels, 1984). Secondly, neither body mass nor swimming stamina were affected by parasitism (Daniels, 1985a). If the parasite exerted some physiological, behavioural or metabolic effect on the lizard to promote diving, it is surprising that the other parameters remained

unaffected. Swimming was the predominant aquatic escape tactic employed by *E. quoyii* and therefore seems a much more suitable mechanism for the parasite to exploit. Acanthocephalans alter the swimming behaviour of many invertebrate intermediate hosts (Holmes and Bethel, 1972; Bethel and Holmes, 1973, 1974, 1977). Parasites also often interfere with the stamina of many vertebrate hosts (Rau and Caron, 1979). Aberrant swimming behaviour may still confer protection from many terrestrial predators while reducing the ability of the lizard to escape from *P. porphyriacus*. Diving is so infrequently practised that even if all the divers I observed were parasitised they represent a barely significant proportion of the total population. In addition, if 5% of the lizard population were divers and all were parasitised, then 85% of the parasitised individuals did not dive.

Thirdly, if *S. rotundocapitatus* actively influences diving, which increases the likelihood of infected lizards being consumed by the snake, then the proportion of the diet of *P. porphyriacus* comprised of parasitised lizards must increase from that predicted by random collection, i.e. from 34% of all *E. quoyii* captured, to a maximum of 100% of the water skink component of the snake diet. However, infected lizards can only increase from 0.68% to 2% of the dietary items of red-bellied black snakes. The snakes do most of their foraging on land, collecting frogs and lizards from holes or undercover on the stream banks (Shine, 1975, 1977). Comparatively few of the prey species of the snake are completely aquatic (Shine, 1977). Hence any parasitic alterations to skink behaviour which promote water utilisation may neither increase nor decrease the likelihood of consumption by the snake.

However, some selective advantages for an active strategy can still exist if the increased utilisation of aquatic escape tactics confers protection from all predators except *P. porphyriacus*. This does not appear likely. Water skinks in the New England region are potential prey items for 101 species of predator (Daniels and Heatwole, 1984). Fifty species are known to consume lizards and include mammals, birds, reptiles, fish and invertebrates. An additional 51 species have been reported to capture other similar sized vertebrates. Of the total 101 potential predators, 27.7% are most likely to capture *E. quoyii* only in water, 11.9% can capture lizards on land or in water, 54.5% are purely terrestrial predators while 5.9% of predators are

fossorial (Daniels and Heatwole, 1984). Thus the use of water as an escape medium still exposes *E. quoyii* to attack from 39 predatory species, several of which are as important, if not more so, than *P. porphyriacus* (e.g. kingfishers and herons).

It seems unlikely therefore that *S. rotundocapitatus* is using active mechanisms to promote the consumption of the transport host by the final host. The only behavioural aberration so far observed in infected lizards is unlikely to affect capture frequency, particularly as the lizards are so rarely eaten by snakes. In addition, as a consequence of any active changes, natural selection may promote host resistance either to the parasite or to the behavioural change. There is always the risk that the response of the host may outweigh any advantage of the changed behaviour, to the detriment of the parasite. All my examinations to date have failed to isolate the intermediate host. However, it is possible that the parasite does not employ any active transfer mechanisms in that host either or that employing active transport mechanisms may not be necessary. I do not know that the parasite affects the first host in the same manner as the second. Many other acanthocephalans influence the behaviour of the first host but are benign in the second. However it is reasonable to hypothesise that passive strategies are the primitive ones from which time and natural selection develop more active methods in some species. As I wish to examine the primitive 'worst case' situation I will assume that in this system transition through the first host is also passive.

Holmes (1976) observed that once in an intermediate host the normal operation of the food web will greatly enhance the probabilities of reaching some potential final host. In the case of *S. rotundocapitatus*, it is possible that the operation of the food web will passively support parasite transfer and enable the establishment of a viable parasite population, provided both the hosts and the worms are long lived. Utilising the knowledge of the ecology of the two vertebrate hosts and the parasite, it is possible to calculate the time required for a parasite population to become established. Assume an infected *P. porphyriacus* enters a riparian habitat previously free of the acanthocephalan. Then *S. rotundocapitatus* eggs become abundant and can retain their infectivity for very long periods until consumed by the intermediate host. Assuming that the abundance of eggs result in the very rapid infection of a substantial proportion of the inter-

mediate host population then there are two crucial periods in the parasite lifecycle. Firstly, the infection of 34% of the *E. quoyii* with cystacanths and then the infection of 23% of the *P. porphyriacus*.

To calculate the time for the passive transfer of the parasite from the intermediate host to the lizard, six assumptions are made: (1) As aquatic prey comprise 1-7% of prey items, we assume 1% of food items are the intermediate hosts; (2) 33% of intermediate hosts are infected; (3) Lizards eat every day; (4) Lizards eat two types of prey/day; (5) Lizards are active 6 months/year; (6) 20% of cystacanths hatch in the lizard and survive to again form a cystacanth. The predicted proportion of infected arthropods is unsubstantiated because the intermediate host is unknown. However, the proportion is similar to the levels of infection observed in the other hosts. Both Daniels (1984, 1987) and Veron (1969a) observed virtually all *E. quoyii* to contain fresh prey. Half of Veron's lizards contained prey from more than five taxa while most of mine had more than two prey items. The value of 20% of cystacanth viability is an estimate, probably an underestimate. About 20% of cystacanths removed from *E. quoyii* and fed to *P. porphyriacus* developed into adults (Daniels, pers. obs.). Thus the time for 34% of *E. quoyii* to become infected with *S. rotundocapitatus*:

$$= (\% \text{ of prey infected}) \times (\% \text{ of prey in diet}) \times (\text{no. prey items/day}) \times (\% \text{ of lizards infected}) \times (\text{viability of cystacanths}) \\ = (100/33) \times (100/1) \times (1/2) \times (34/100) \times (100/20) \\ = 258 \text{ days or approximately one year}$$

Because lizards are only active 6 months/year, it takes about 1.5-2 years for 34% of *E. quoyii* to become infected.

To calculate the time for 23% of *P. porphyriacus* to become infected it is necessary to make five assumptions; (1) Snakes eat one prey item at a time; (2) Snakes eat once every three days; (3) 34% of *E. quoyii* contain cystacanths; (4) 20% of cystacanths exsheath and survive to reproduce in *P. porphyriacus*; (5) Snakes are active 6 months/year. A third of 22 *P. porphyriacus* I examined had prey in their stomachs, although Shine observed that a greater percentage of his snakes had fed recently (Shine, 1977). I usually found one prey item/snake although the average in Shines' was nearly three (Shine, 1977). *P. porphyriacus* probably feed more often than assumed here. Thus the time for 23% of *P. porphyriacus* to become infected is:

$$= (\text{no. of prey eaten/feed}) \times (\text{frequency of eating}) \times (\% \text{ of snakes infected}) \times (\text{viability of cystacanths}) \times (\% \text{ of lizards infected}) \\ = (1) \times (3) \times (100/2) \times (23/100) \times (100/20) \times (100/34) \\ = 507 \text{ days}$$

Snakes are active for only half of the year so it takes approximately 3 years for 23% of the snake population to become infected. The total time for a parasite population to become established in all hosts is therefore 5-6 years, well within the lifespan of both the lizard and the snake, the more so considering the conservative nature of the calculations.

However, can the parasites maintain their numbers in two reptilian hosts in the face of natural mortality and the short activity period? Assuming lizards live 6 years then 17% of the population die each year. On third of that, or 6% of the total lizard population die containing parasites. (This is probably an overestimate because during any year, most mortality within the *E. quoyii* population occurs amongst the juveniles, which are not parasitised (Veron, 1969a; Daniels, 1984). Thus, to maintain the population stability *S. rotundocapitatus* must infect 6% of the uninfected lizards/year;

$$= (\% \text{ of prey in diet}) \times (\% \text{ of prey infected}) \times (\text{prey items eaten/day}) \times (\% \text{ of lizards infected}) \times (\text{viability of cystacanths}) \\ = (100/1) \times (100/33) \times (1/2) \times (6/100) \times (100/20) \\ = 45 \text{ days}$$

But 28% of the surviving population is already infected. Thus, the time for infection:

$$= 45 \times c. 125/100 \\ = 56 \text{ days or approximately 2 months}$$

Similarly if snakes live 10 years then the population turnover is 10%/year with approximately 2.5% of the population dying while containing parasites (again an overestimate because the greatest mortality occurs amongst juveniles which are relatively unparasitised (Shine, 1978; Daniels, 1984). Therefore, for population stability, approximately 2.5% of the uninfected snakes must collect a parasite/year. Thus the time for infection:

$$= (\% \text{ of prey in diet}) \times (\text{prey eaten at a time}) \times (\text{no. days between feeding}) \times (\% \text{ of snakes infected}) \times (\text{viability of cystacanths}) \times (\% \text{ of lizards infected}) \\ = (100/2) \times (1) \times (3) \times (2.5/100) \times (100/20) \times (100/34) \\ = 107 \text{ days}$$

= 55 days

However, 20% of the surviving population is already infected. Therefore the time for infection:

= $55 \times 120 / 100$

= 66 days or approximately 2 months

Hence it takes approximately 4 months for the parasite to replace individuals lost when their hosts die. Four months is well within the yearly activity period of the reptiles, the more so considering the conservative nature of the calculations.

This study supports the hypothesis that the operation of the food web will passively transport the parasite from one stage in its life cycle to the next. The time predicted is probably an overestimate. However, as acanthocephalans have separate sexes, it is crucial for at least 2 worms to reach each snake. The number of cystacanths per lizard is not important. The conservative basis within the calculations provides excess time which may be important for allowing extra parasites to infect hosts. Moreover, the great longevity of *P. porphyriacus* may compensate for the low rate of consumption of *E. quoyii* and enable populations of *S. rotundocapitatus* to become established in each infected snake.

Perhaps the most convincing evidence for the utilisation of the passive transfer mechanism involves the very low numbers of parasite/host. It is possible that the low numbers of parasites per host represent a truncated negative binomial distribution because host mortality may be associated with increasing intensity of infection. However, no pathological effects were observed in either host, even in the skink with 8 parasites (Daniels and Simbotwe, 1984). Other animals appear to be capable of supporting large numbers of acanthocephalans without discernible effect (Holmes, 1982). Hence, parasites practising passive strategies rely on time and the laws of probability to promote infection. As each infection is an independent event, then the structure of the parasite population should be characterised by many infected hosts containing relatively few individuals. The distribution of *S. rotundocapitatus* in both *E. quoyii* and *P. porphyriacus* clearly falls into the passive type.

Parasites can increase the probability of transfer and promote the success of the passive mechanism in three ways. Firstly, by prolonging the survival time and viability of the eggs, cystacanths and adults. In some acanthocephalan species the eggs retain their infectivity for more than 3 years (Crompton, 1975) while acanthellae

at least 6 months old have been removed from cystacanths in *E. quoyii* (Daniels and Simbotwe, 1984). Longevity is crucial because of the slow rate of transfer between hosts. However, a prolonged survival time is especially important for cystacanths and adult worms because of the long hibernation periods of their hosts. Host hibernation results in long periods of food unavailability for adult *S. rotundocapitatus* and reduces mating opportunities because of the delay in the rate of acquisition of more parasites.

Hibernation also affects reproduction because it stops the release of eggs into the correct aquatic habitats. Adult worms must either live a long time and be capable of producing large numbers of eggs or live a short time and produce very large numbers of long lived eggs in order to maximise reproductive output and compensate for the high attrition rate in this type of life cycle.

It is also crucial for cystacanths to be capable of exsheathing, transferring and establishing themselves in the next host when the opportunity arises. The value of 20% used in my calculations may be unrealistically low. A doubling of this percentage incurs a major reduction in the time necessary to establish a parasite population. Cystacanth viability is probably the most important variable in the population dynamics of the parasite because it is the most malleable. Without a high cystacanth viability it is unlikely that enough cystacanths would reach the final host in time to develop into adults, mate and maintain egg production.

Secondly, the passive transfer mechanism could be promoted if the parasite was not specific to one intermediate or transport host. In situations where both the transport host and the final host consume a wide range of prey items all at a low frequency, parasites will transfer more rapidly from one host to the next by using many host species rather than by increasing the level of infection within one specific host. Therefore, cystacanths should tolerate a relatively broad range of physiological conditions in order to survive in many different types of host. Cystacanths of *S. rotundocapitatus* have been extracted from two other small skinks, *Hemiergis decresiensis* and *Lampropholis guichenoti* but in both cases the level of infection was less than 6% (Daniels and Simbotwe, 1984). Undescribed acanthocephalan cystacanths have also been extracted from other snakes and lizards (Johnston and Deland, 1929a). However, somewhat surprisingly, cystacanths have not been collected from frogs. From a transfer viewpoint, frogs

would be better transport hosts than lizards because they are more important dietary items for *P. porphyriacus*. However, it appears either that *S. rotundocapitatus* cystacanths cannot survive in other animals, or the consumption of infected *E. quoyii* is sufficient to maintain the parasite population.

The third mechanism available to *S. rotundocapitatus* to promote the passive transfer mechanism involves exploiting behavioural variability within the host population. The presence of parasites in water skinks with extended voluntary diving times may reflect such an exploitation. The tendency to dive may vary greatly between animals within a population. Long dives might be characteristic of lizards which use the water most frequently as an escape medium and also as a food source. These more aquatic lizards may be more likely to feed at the waters' edge, capture aquatic prey and thus become infected with *S. rotundocapitatus*. When attacked, the more aquatic lizards may exhibit a greater tendency to swim or dive, conferring a degree of protection from terrestrial predators but not from *P. porphyriacus* (Daniels, 1985a). Thus the parasite can exploit a polytheism within the host population to increase the chance of reaching the final host. The presence of *S. rotundocapitatus* correlates with, rather than causes, a behavioural or physiological difference and is therefore less likely to stimulate host resistance.

Active transfer mechanisms can be disadvantageous when the intermediate host represents a small proportion of the diet of the final host, the final host consumes a wide variety of prey and the intermediate host is a prey item for a large range of different predators. This type of food web is common in Australian ecosystems and specialist systems involving one predator and one prey are rare (although there are a number of vertebrates which specialise on ants or termites). The relative absence of simple food webs, especially amongst the vertebrates may be a result of the low vertebrate biomass. It may be impossible for one carnivore to specialise on one, or a few, prey species because the densities of the latter are too low. The optimal transport strategies for parasites in diffuse and complex food webs are often passive rather than active, provided reproductive output remains high enough to compensate for the attrition.

ACKNOWLEDGEMENTS

This paper grew from discussions with

Richard E. Lenski and Karen M. Calloway to whom I am particularly grateful. A.F. Bennett, T. Garland, J.J. Schall, J.C. Holmes and R. Shine also provided comments and criticisms. Julie Dodwell and Karen Rowe typed the manuscript.

LITERATURE CITED

- BETHEL, W.M. AND HOLMES, J.C. 1973. Altered evasive behaviour and responses to light in amphipods harbouring acanthocephalan cystacanths. *J. Parasit.* 59: 945-956.
1974. Correlation of development of altered evasive behaviour in *Gammarus lacustris* (Amphipoda) harbouring cystacanths of *Polymorphus paradoxus* (Acanthocephala) with the infectivity to the definitive host. *J. Parasit.* 60: 272-274.
1977. Increased vulnerability of amphipods to predation owing to altered behaviour induced by larval acanthocephalans. *Can. J. Zool.* 55: 110-115.
- BRASSARD, P., RAU, M.E. AND CURTIS, M.A. 1982. Parasite-induced susceptibility to predation in diplostomiasis. *Parasitology* 85: 495-501.
- CLARKE, B.D. 1979. The evolution of genetic diversity. *Proc. R. Soc. Lond. B.* 205: 453-474.
- CROMPTON, D.W.T. 1970. 'An ecological approach to acanthocephalan physiology.' (Cambridge Univ. Press: Cambridge). 125 pp.
1975. Relationships between Acanthocephala and their hosts. *Symp. Soc. Exp. Biol.* 29: 467-504.
- DANIELS, C.B. 1984. The adaptations to a riparian habitat by the eastern water skink *Sphenomorphus quoyii*. (Unpublished Ph.D. thesis., University of New England).
- 1985a. The effect of infection by a parasitic worm on swimming and diving in the water skink *Sphenomorphus quoyii*. *J. Herpet.* 19: 160-162.
- 1985b. The effect of tail autotomy on the exercise capacity of the water skink *Sphenomorphus quoyii*. *Copeia* 1985: 1074-1077.
1987. Aspects of the aquatic feeding ecology of the riparian skink *Sphenomorphus quoyii*. *Aust. J. Zool.* 35: 253-258.
- DANIELS, C.B. AND HEATWOLE, H. 1984. The predators of the water skink *Sphenomorphus quoyii*. *Herpetofauna.* 16: 6-16.
1990. Factors affecting the escape behaviour of a riparian lizard. *Mem. Qd Mus.* 29(2): 375-387.
- DANIELS, C.B. AND SIMBOTWE, M.P. 1984. The biology of acanthocephalan parasites of Australian skinks. *J. Herpet.* 18: 211-213.
- DONE, B.S. AND HEATWOLE, H. 1977. Social behaviour of some Australian skinks. *Copeia*

- 1977: 420-430.
- FLEAY, D. 1937. Black snakes in combat. Proc. R. Zool. Soc. N.S.W. 1936/37: 40-42.
- GILBERT, P.A. 1935. The black snake (*Pseudechis porphyriacus*, Shaw). Proc. R. Zool. Soc. N.S.W. 1935/35: 35-37.
- HOLMES, J.C. 1976. Host selection and its consequences. pp. 21-39. In Kennedy, C.R. (ed.), 'Ecological aspects of parasitology.' (North Holland Publ. Co.: Amsterdam).
1982. Impact of infectious disease agents on the population growth and geographical distribution of animals. pp. 37-51. In Anderson, R.M. and May, R.M. (eds.), 'Population biology of infectious diseases.' (Springer-Verlag: Berlin).
- HOLMES, J.C. AND BETHEL, W.M. 1972. Modification of intermediate host behaviour by parasites. Zool. J. Linn. Soc. 51:123-149. Suppl. 1.
- JOHNSTON, T.H. 1911. A census of Australian reptilian entozoa. Proc. R. Soc. Qd 22: 232-249.
1913. Notes on some entozoa. Proc. R. Soc. Qd 24: 62-109.
- JOHNSTON, T.H. AND DELAND, E.W. 1929a. Australian Acanthocephala No. 1. Census of recorded hosts and parasites. Trans. R. Soc. S. Aust. 53: 146-152.
- 1929b. Australian Acanthocephala No. 2. Trans. R. Soc. Aust. 53: 153-166.
- MOORE, J. 1984. Altered behavioural responses in intermediate hosts. An Acanthocephalan strategy. Amer. Nat. 123: 572-577.
- MORRIS, S.C. AND CROMPTON, D.W.T. 1982. The origins and evolution of the Acanthocephala. Biol. Rev. 57: 85-115.
- RAND, A.S., GUERRERO, S. AND ANDREWS, R.M. 1983. The ecological effects of malaria on populations of the lizard *Anolis limifrons* on Barro Colorado Island, Panama. pp. 455-471. In Rhodin, A.G.J. and K. Miyata, K. (eds), 'Advances in herpetology and evolutionary biology.' (Mus. Comp. Zoology: Cambridge, Massachusetts).
- RAU, M.E. AND CARON, F.R. 1979. Parasite-induced susceptibility of moose to hunting. Can. J. Zool. 57: 2466-2468.
- SCHALL, J.J. 1983. Lizard malaria: Parasite-Host ecology. pp. 84-100. In Pianka, E.R., Huey, R.B. and Schoener, T.S. (eds.), 'Lizard ecology: Studies of a model organism.' (Harvard Univ. Press: Cambridge, Massachusetts).
- SCHMIDT, G.D. AND KUNZ, R.E. 1966. *Sphaerechinorhynchus serpenticola* sp. nov. (Acanthocephala: Sphaerechinorhynchinae) a parasite of the Asian cobra *Naja naja* (Cantor) in Borneo (Malaysia). J. Parasit. 52: 913-916.
- SHINE, R. 1975. Ecological studies on Australian elapid snakes. (Unpublished Ph.D. thesis, University of New England).
1977. Habitats diet and sympatry in snakes: A study from Australia. Can. J. Zool. 55: 1118-1128.
1978. Growth rates and sexual maturation in six species of Australian elapid snakes. Herpetologica 34: 73-78.
- SMITH-TRAIL, D.R. 1980. Behavioural interactions between parasites and hosts: Host suicide and the evolution of complex life cycles. Amer. Nat. 116: 77-91.
- SPELLERBERG, I.F. 1972. Thermal ecology of allopatric lizards (*Sphenomorphus*) in south-east Australia. III. Behavioural aspects. Oecologia 11: 1-16.
- VERON, J.E.N. 1968. Aspects of the role of temperature in the ecology of the water skink *Sphenomorphus quoyii*. (Unpublished M.Sc. thesis, University of New England).
- 1969a. An analysis of the stomach contents of the water skink *Sphenomorphus quoyii*. J. Herpet. 3: 187-189.
- 1969b. The reproductive cycle of the water skink *Sphenomorphus quoyii*. J. Herpet. 3: 55-63.
- VERON, J.E.N. AND HEATWOLE, H. 1970. Temperature relations of the water skink *Sphenomorphus quoyii*. J. Herpet. 4: 141-153.